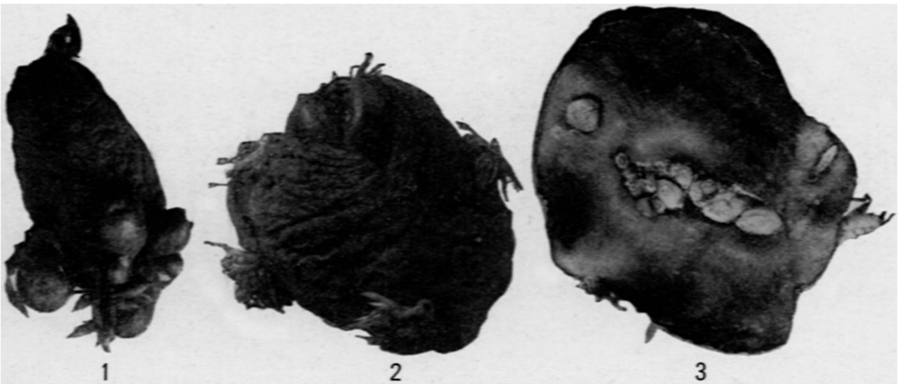
INGROWING SPROUTS OF SOLANUM TUBEROSUM[1]

C. STUART GAGER

(WITH PLATE XXXVI AND SIX FIGURES)

Description

As is well known, it is not at all uncommon to find tuberization of the sprouts on potatoes kept over winter in a cellar. The fact is commonly attributed to the absence of light and the dampness of the cellar. In the late fall of 1907, a large basket of potatoes, of the "Green Mountain" variety, was placed, for want of a cellar, in an unheated chamber. There was one east window in the room,



FIGS. 1–3.—Fig. 1, Various stages of tuberization of the sprouts of a potato under conditions of diffuse illumination; fig. 2, Young tubers emerging from within an old seed tuber of *Solanum tuberosum* (cf. figs. 1, 4, and 5); fig. 3, Cross-section of a tuber of *Solanum tuberosum* with ingrown sprouts.

and the curtain was ordinarily up, so that the room was neither dark nor damp. On the contrary, the atmosphere of the room was comparatively dry. Under these conditions, a number of the potatoes were found with sprouts in various stages of tuberization, varying from a slight enlargement back of the tip to well formed "potatoes" (fig. 1), but in the case of two or three of them, the

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sprout-tubers appeared to be emerging through the skin from within the potato (fig. 2). Closer observation and dissection disclosed the interesting fact that at least a quarter or a third of the potatoes, of which there was about a bushel in all, had ingrowing sprouts. The condition is well illustrated in fig. 3, which is a typical cross-section.

On careful dissection of many of the tubers, the ingrowing sprouts were found to ramify in every direction throughout the

FIG. 4.—Tubers of *Solanum tuberosum* with ingrowing sprouts: the figure at the right shows the ingrown sprouts emerging through the skin; the figure at the left is of a dissection, showing rootlets, the marked development of lenticels, and the tuberization of some of the branches of the ingrown sprouts within the old tuber (cf. figs. 2 and 5).

tissue of the potato. The atrophied and etiolated bud end retained the characteristic nutation curvature, but the sprout was frequently more or less enlarged just back of the tip (figs. 4 and 5). Lenticel-like openings were well developed in the epidermis of the sprouts, often giving them the appearance of a cylindrical file.

Numerous fibrous roots grew out from the branches, and they seemed, for the most part, to be confined in their growth to the channels made by the stem. As is clearly shown in the right hand

potato of fig. 4, the internal sprouts would often grow through the skin and emerge at various points.

The branches tuberized freely, and it was not uncommon to find five or six, or even more, well formed, but pure white, tubers of various sizes entirely within the old tuber. In some cases, as in the right hand specimen of fig. 5, the branches were only imperfectly tuberized, and the tip retained its nutation curvature. Often, as noted above, the young tubers, like the unswollen branches, had pushed through the skin of the potato and, where exposed to the air, had developed a characteristic brown epidermis (fig. 4).

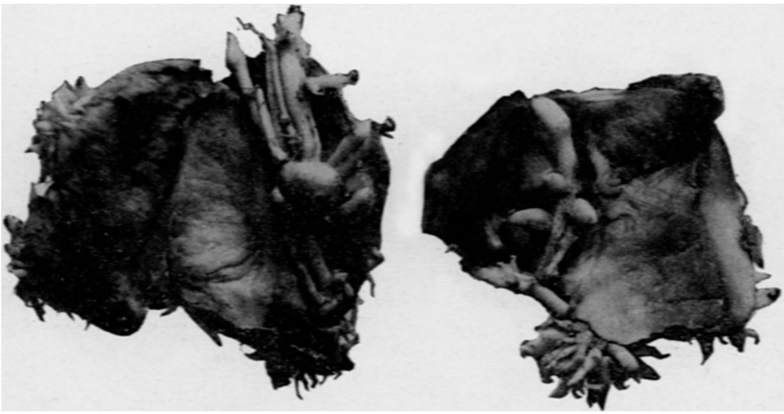

FIG. 5.—Dissected tubers of *Solanum tuberosum*, showing various stages of tuberization of branches of ingrown sprouts, both within and without the seed tuber (cf. figs. 2 and 4).

In many instances there was every *appearance* of a reversal of polarity of the sprout. This is clearly shown in fig. 6, which illustrates two "eyes," the one at the left of a normal potato, the one at the right of one of the abnormal ones. What has occurred in the latter *appears* to be just the reverse of what took place in the former: roots occur at the distal end of the sprout, where we would ordinarily expect the terminal bud, and the numerous branches appear to have developed from the proximal end of the sprout. Whether this is actually the case or not one hesitates to say. It is possible that the entire shoot system, shown at the right in fig. 6, may have developed from a sprout whose tip turned through 180°

toward the surface of the potato and penetrated the parent tuber from without. But it is only the a-priori improbability of a reversal of polarity that makes the writer hesitate to declare it. The evidence clearly indicates it, but the evidence is not all in.

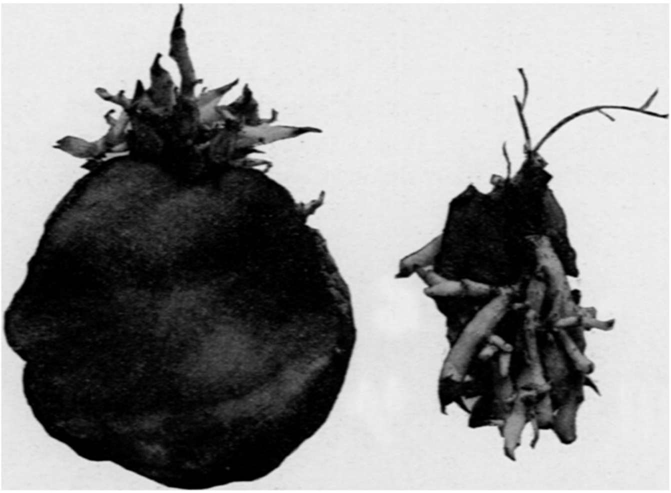

Fig. 6.—Sections through sprouting tubers of *Solanum tuberosum:* at the left, a normal "eye"; at the right, an "eye" with sprouts ingrown and indicating a reversal of polarity of the branch.

Discussion

What caused the ingrowing of these sprouts it is difficult to say. The fact that the potatoes were stored in a room where the air was much drier than that of cellars, where potatoes are usually kept, suggests that the low humidity was at least a contributory cause. But equally interesting is the question of how the sprouts made their way through the tuber. Were the channels through which they grew formed by the digestion of the potato tissue by an enzyme secreted by the tip of the sprout; or did the channels result merely from the mechanical pressure of the sprout as it elongated?

It will be recalled that a similar problem arose in connection with the endogenous emergence of lateral roots. Considerable difference of opinion has existed on this question. The first physiological study of the emergence of lateral roots appears to have been made in 1871, by Reinke (9), who stated that the channel

through the cortex was digested by a substance secreted by the emerging root. The same conclusion was reached later by VON HÖNE (12) and by VAN TIEGHEM (11). Neither REINKE'S nor VAN TIEGHEM'S figures, however, show evidence of enzymatic action. In 1896 CZAPEK (1) reported that he found in the excretions of the roots of higher plants no evidence of any enzymes. If they are present, the amounts are too small to be detected. PFEFFER has declared for a mechanical *modus operandi*, aided by some activity on the part of the cortical tissue.

In 1894 PEIRCE (6) found that the roots of *Vicia* and *Pisum* penetrated living tissue by mechanical pressure, unaided by enzymes. He also states that the radicle of *Pisum* could enter through the uninjured periderm of a potato from the outside. In 1903 OLUFSEN (5) reported a confirmation of PEIRCE'S results, but POND (8) was unable to confirm them, and reported negative results also for *Vicia Faba* and *Lupinus albus*. When the periderm was wounded, the radicles of these seedlings entered easily and penetrated the parenchymatous tissue. When the periderm was unwounded, the radicles deeply indented the surface, but never pierced through. Microscopic examination showed that the periderm cells, and, to a less degree, the hypodermal cells also, were compressed, but there was no evidence of corrosion. "The advancing root formed callus, but when the periderm is wounded the callus does not form. . . . . "

In one of POND'S experiments a potato tuber was cut in two and the outer surfaces placed together and held firmly in this position by string. Then a channel was made in one half to within a few millimeters of the skin, and the radicles of seedlings inserted. The whole was then incased in gypsum. The radicles perforated the periderm of the first half from the inside, and were thus brought into contact with the outside of the periderm of the other half, but this they failed to penetrate. From these observations POND concludes that the mechanical push is too weak to accomplish penetration from without. "Microscopical examination of the flesh of a potato showed no evidence of any digestive action."

In a similar manner POND found that an elongating radicle of *Lupinus albus* was unable to penetrate through the uninjured

epidermis of another *Lupinus* radicle. The second radicle was always deeply indented, but no signs appeared of corrosion of the surface. If the surface was even very slightly wounded, as for example by pricking it with a fine glass point, then the other radicle easily entered and passed entirely through without callus formation. The penetrating root, however, was never found to pass through the central cylinder, but always around it, thus indicating more resistance than that offered by the cortex. The cylinder was indented, but there was no evidence of corrosion of its cells. Starch grains did not appear digested either by autolysis or by the entered root. The results of mechanically forcing a glass rod into the tissue could not be distinguished from those produced by an entering radicle. The conclusion drawn was that the mechanical push was not sufficient to pierce the cuticle from the outside, and that "if the radicle or the lateral root secretes an enzyme, such enzyme has no digestive action upon the cuticle."

As in the case of the roots, so with the potato, the course of procedure for a solution of the problem is clearly indicated. If the channels were the result of enzymatic action we would expect to find, first, in the tips of the sprouts an enzyme able to digest the potato tissue; second, evidence of enzymatic action in the tissue itself; third, absence of any evidence of mechanical pressure; and finally, we might expect to find the epidermis of the ingrowing sprout modified in the direction of glandular epithelium. If the sprout merely pushed its way through the tissue of the tuber, we would find no signs of enzymes or of enzymatic action, but rather positive indication of mechanical pressure.

Physiological and anatomical study

A considerable quantity of tips of the ingrowing sprouts was given to Professor WILLIAM J. GIES, of Columbia University, who kindly offered to have them tested for enzymes. While waiting for a report on this test, microscopic sections of the sprouts were examined, to see if there was any modification of the epidermis in the direction of a glandular epithelium, such for example as that on the scutellum of the embryo of *Zea Mays*. As is clearly shown in *A* and *B* of plate fig. 1, a well developed columnar epithelium was

found, and since the epidermal cells are more nearly isodiametric in normal sprouts, it was expected that the chemical examination would disclose the presence of enzymes. Such however was not the case. No enzymes were detected, and this experience emphasizes the truth that any inference as to the function of an organ or tissue, based upon structure alone, cannot always be relied upon, unless substantiated by positive evidence.

Further confirmation of the absence of enzymatic action was obtained by examining microscopic sections of the walls of the channels made by the sprouts in the tissue of the tuber. There were no signs of corrosion of the cell walls nor of the starch grains within the cells (plate fig. 2).

Only one alternative remained: the sprouts made their way through the tissue of the tuber by mechanical pressure alone. This conclusion found abundant confirmation. The wall cells of the channels made by the sprouts were greatly compressed by the advancing tip (plate figs. 2 and 4). In light of the studies made on the mode of emergence of lateral roots, it is instructive to compare plate figs. 3 and 4. This latter figure is a detail of the tissues at the point marked *C* in plate fig. 1. Fortunately, at this point a lateral root had begun to develop, and it is clearly seen (fig. 3), not only that the walls of the cortical cells show no signs of enzymatic action, but that they are evidently compressed by the advance of the developing root tip. The paths of the ingrowing sprouts and of emerging lateral roots are evidently made in the same manner, namely by mechanical pressure alone, unaided by enzymatic action.

Experimental production of ingrowing sprouts

But how did the ingrowing sprouts start? Do they, as suggested above, represent normal sprouts that for some unexplained reason turned their tips toward the tuber and penetrated through the skin? There is no evidence for this view. In numerous cases where the "eyes" were deeply indented, small sprouts grew out laterally until their tips came into contact with the skin of the potato. But, as in the case of POND's attempt to cause one root of *Lupinus* to penetrate another held firmly at right angles to it, so here the surface of the potato was indented by the tip

of the sprout, but no case of penetration was observed. At the writer's suggestion, Miss LUCILE KEENE,[2] then a senior in the University of Missouri, endeavored to secure the penetration of one potato by the sprouts of another. The two tubers were bound tightly together with stout cord, and buried in moist sphagnum. In no case were the sprouts successful in penetrating through the uninjured skin of the adjacent tuber, though the latter was indented. However, if the sprouts were placed against the cut surface of another potato, they entered easily, made their way through the parenchymatous tissue to and *through* the skin at the farther surface. That the sprouts can easily penetrate the cortex from within, though not from without, was shown by the abnormal cases where such penetration was general (fig. 4). Had enzymolysis been a factor, the sprouts might as easily have penetrated from without. The experiments with roots, as noted above, gave analogous results.

The observed facts will not admit of a definite denial of reversal of polarity. Many of my dissections cannot reasonably be interpreted in any other way, but it still seems possible, though not always probable, that the ingrown sprout arose as a lateral branch starting at the very base of the main sprout and *below the skin of the tuber*. This hypothesis at least does not make as large a draught on pure faith as one involving the conception of a reversal of polarity in the shoot. DETMER (**2**) long since called attention to the fact that while the intensity of polarity varied greatly with different species, it was especially well marked in the case of *Solanum tuberosum*.

The cause of tuber-formation

What caused some of the ingrown sprouts to form tubers? The answer to this question is of course bound up with the larger question as to why potato branches ever tuberize. The literature bearing on this problem was discussed by the writer (**3, 4**) in 1906, and need not be reviewed here. Reference may again be made, however, to the suggestion of BERNARD that the formation of tubers is due to a species of *Fusarium*, endotropic with *Solanum tuberosum*.

[2] Miss KEENE also found a similar case of ingrowing sprouts in Montana, but the sprouts were only slightly branched, and formed no tubers within the old potato.

This suggestion was tested experimentally by JUMELLE, but with negative results. Quite evidently this factor does not enter in the tuberization of branches of the ingrown sprouts. GOEBEL cites tuber-formation as an illustration of "qualitative correlation," stating that it is a function of the relation of the branch to the whole shoot system, its underground position, and the material supplied to it.

It seems to the writer that an attempt to explain such a deep-seated character as the formation of tubers by potato plants is like trying to explain the cornness of corn. We may ascertain experimentally what external conditions or combination of circumstances must be realized in order that tubers may result, but that they form at all is because the plant is *Solanum tuberosum*, rather than *Pisum sativum* or *Solanum Dulcamara*. To use a recent and very valuable terminology, the formation of tubers by *Solanum tuberosum*, or by any other tuber-forming species, under suitable environmental conditions, *is an expression of the genotypical constitution of the plant.* Further explanation than this lies far in the future.

Conclusion

1. Ingrowing sprouts of *Solanum tuberosum* make their way through the tissue of the tuber not by enzymatic digestion of a channel in the tissue, but by the mechanical pressure which accompanies growth in length.

2. Potato sprouts do not elongate with force sufficient to penetrate through the uninjured "skin" of the potato tubers from the outside, but they easily penetrate the skin from the inside.

3. A reversal of polarity in ingrowing potato sprouts is not definitely demonstrated, but there is evidence pointing to this conclusion.

4. Tuberization of branches takes place freely on ingrown sprouts of *Solanum tuberosum.*

5. The formation of tubers on *Solanum tuberosum* is a function of external conditions plus the genotypical constitution of the species.

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EXPLANATION OF PLATE XXXVI

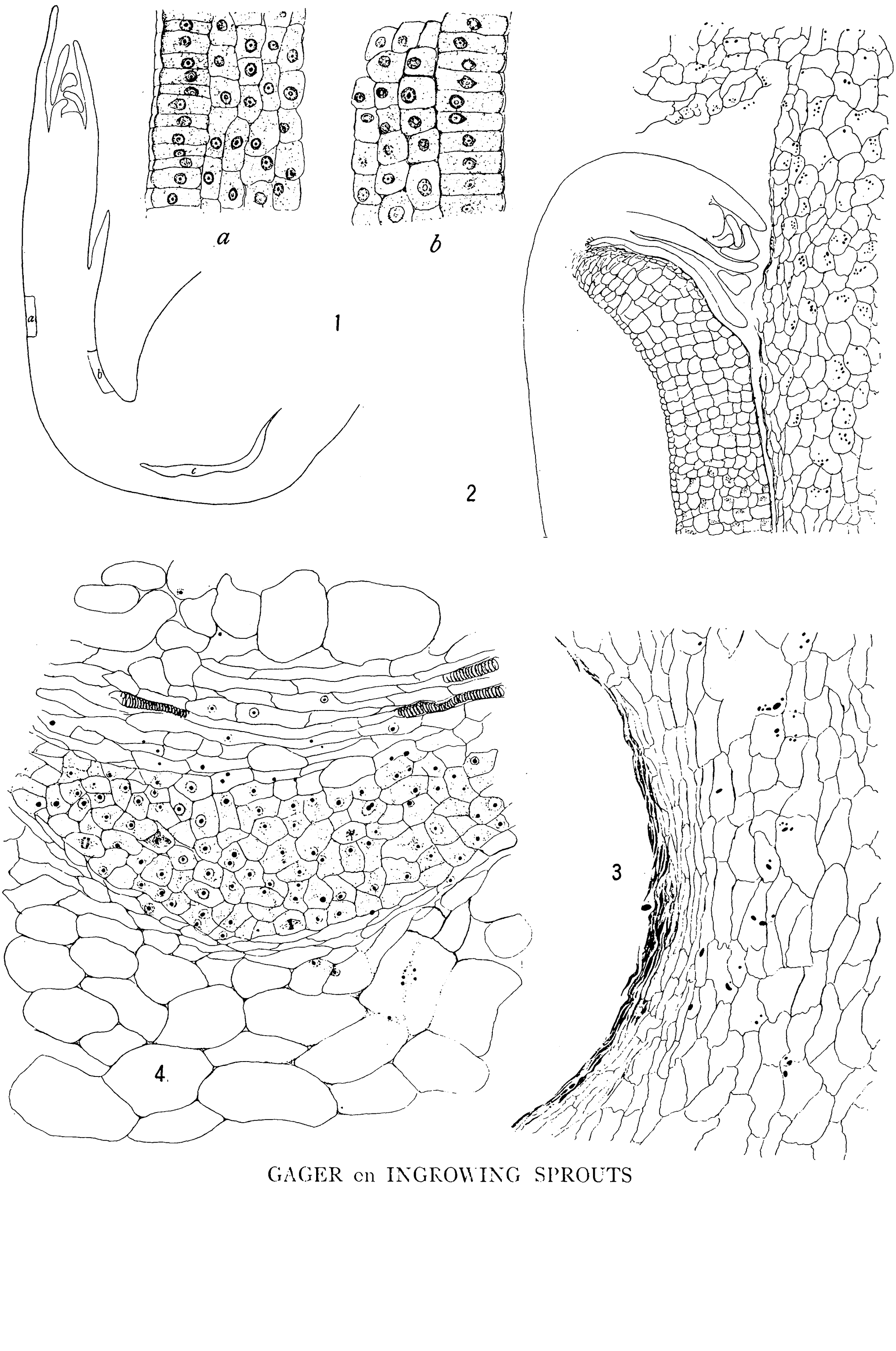
Solanum tuberosum

FIG. 1.—Outline of a longitudinal section of an ingrown sprout: *A* and *B*, cellular structure at the regions marked *A* and *B* in the outline, showing well developed columnar epithelium.—Zeiss oc. 4; obj. D.

FIG. 2.—Longitudinal section through the tip of an ingrown sprout, with adjacent tissue of the seed tuber, showing mechanical compression of the cells of the tuber by the growing sprout and absence of any evidence of corrosion of either cell walls or starch grains; the breaks in the cell walls are artifacts; many of the starch grains have fallen out of the section.—Cf. figs. 3 and 4.—Zeiss oc. 4; obj. AA., lower lens only.

FIG. 3.—Early stage in the development of a root within an ingrown sprout; this section was taken at the area marked *C* in fig. 1; note the compression of the cortical cells by the advancing root.—Cf. figs. 2 and 4.—Zeiss oc. 4; obj. AA.

FIG. 4.—Cross-section through a seed tuber, showing compression of the wall cells of a channel made by an ingrown sprout.—Cf. figs. 2 and 3.—Zeiss oc. 4; obj. AA.



GAGER on INGROWING SPROUTS